

3.0016 SEXUAL DIMORPHISM IN THE HEAD STRUCTURE OF MUTILLIDAE HYMENOP- TERA: A POSSIBLE BEHAVIORAL EXPLANATION¹

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A striking sexual dimorphism involving modifications of the clypeus of males occurs in many species of Mutillidae. This dimorphism is especially pronounced in members of the genus *Timulla*, and is often diagnostic of the species (Mickel, 1937). For example, most of the lower median clypeal surface of *T. vagans* (Fabricius) forms a shallow, smooth, transverse concavity, while the upper median margin is elevated into an arcuate ridge which slopes smoothly into the concave area (Fig. 1). In males of *T. dubitata* (Smith), however, the smooth concave portion does not extend as far laterally, and the ridge rises more abruptly (Fig. 2). In addition to these specializations, the males of some species show a modification in the basic structure of the mandibles. Those of *T. vagans*, for example, are strongly excised beneath, have a large tooth near the base, and have the dorsal surface flattened (Fig. 1). In *T. dubitata* the excised area is absent, the tooth is poorly developed, and the dorsal surface lacks the large flat area (Fig. 2). To my knowledge no attempt has yet been made to provide a functional explanation for these peculiarities of structure. A recent observation of a portion of the courtship behavior of *T. dubitata* has suggested that the adaptive value of the peculiar head modifications of the males of some mutillids may be found in a study of the details of their reproductive behavior. A survey of the scanty literature dealing with this behavior in mutillids provides additional support for this idea.

The first significant report of courtship in the Mutillidae was by Bischoff (1927), who stated that mating in mutillids takes place in flight. The method of carriage was not mentioned. Crevecoeur (1930) presented a detailed description of the mating behavior of the European species *Smicromyrme rufipes* Fabricius. He reported that mating in this species

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occurs on the ground, although the male often flies some distance with the female grasped in his mandibles prior to copulation. Well developed mandibular teeth are present in this species and apparently aid in grasping the female. Creveceur stated that the male tries to grasp the female's pronotum with his mandibles and catch its lateral borders with the mandibular teeth. Immediately preceding copulation in this species the male, carrying the female in his mandibles, climbs a small herbaceous stem and it is there that copulation takes place.

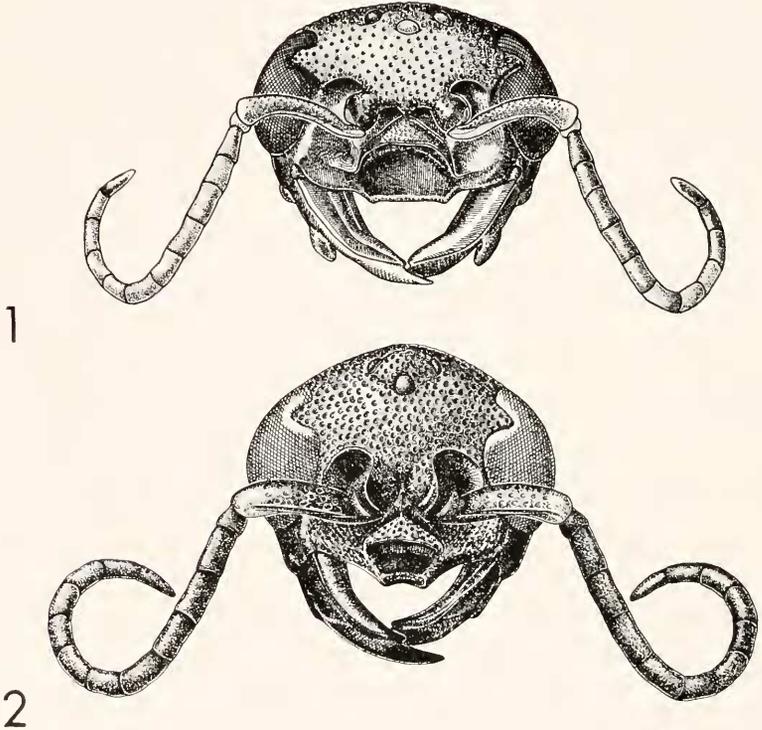
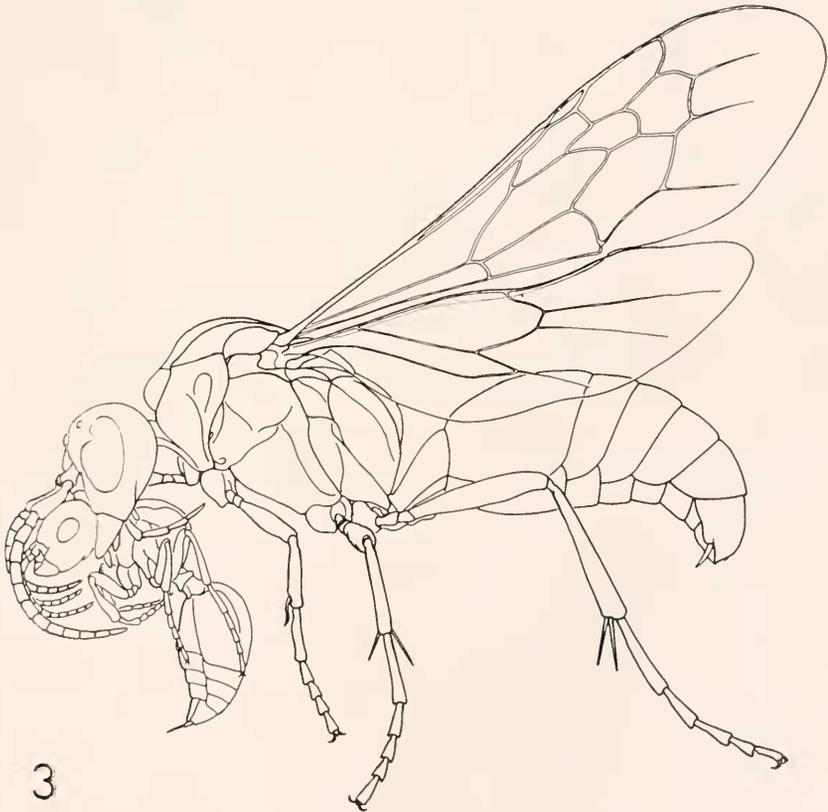


FIG. 1. Head of male mutillid wasp *Timulla vagans* (Fabricius). FIG. 2. Head of male mutillid wasp *Timulla dubitata* (Smith).

Only two observations of the mating behavior of American Mutillidae have been reported. Linsley (1960) observed a mating pair of *T. oajaca* (Blake) in which the male was carrying the female in flight by means of his legs and affixed genitalia. He did not mention any use of the mandibles. A more detailed account of the courtship behavior of *Sphaerophthalma blackeii* (fox) was presented by Ferguson (1962). When a virgin pair

of this species was confined under a 65 mm diameter petri dish the male, upon overtaking the female from the rear, "climbed on her back, seized her neck region with his mandibles, and her body with some of his legs." He then prodded the tip of her abdomen with his extruded genitalia.

During the summer of 1967 at Mason State Forest, near Havana, Illinois, I observed an attempted mating of *T. dubitata*. Upon capturing a large male, which had been flying at a height of about three feet, I discovered that it was carrying a female less than half its size in its mandibles. The female was grasped by the male's mandibles in her cervical region (Fig. 3). Whether or not his legs were used to support her while in



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FIG. 3. Mandibular carriage in *Timulla vagans* (Fabricius)—as preserved, the male (winged) having been pinned. The relative positions of *Timulla dubitata*, discussed in the text, are the same. The specimens illustrated here were collected by H. A. Scullen at Ames, Iowa and are located in the Oregon State collection.

flight was not observed. Shortly after the pair was placed in a 2 dram vial, the male began copulatory attempts while still grasping the female in his jaws. These attempts consisted of shaking the female from side to side violently five or six times and then stroking her sides with his fore legs while standing on his middle and hind legs. After a few seconds of stroking he curved the tip of the abdomen down and forward and prodded the tip of the female's abdomen, apparently attempting to induce her to open her genital chamber. After a few seconds of unsuccessful prodding the sequence was repeated. During the prodding the male's antennae were extended forward over the female's head and were bent down and back so as to press against her venter. Occasionally his antennae were lifted straight up and held rigid. After several minutes of futile attempts the male dropped the female.

DISCUSSION

The importance of the concave clypeal surface of the male becomes apparent when the details of the mandibular carriage of the female by the male are examined. In *T. dubitata*, when the male grasps the female's cervix with his mandibles the convex postocular ridge of the female rests against the male's concave clypeus. This adaptation serves to reduce a point of friction and may, in fact, "lock" the female into the correct position for subsequent steps in the behavioral pattern.

Once the behavior pattern of grasping the cervix of the female by the male's mandibles has arisen in a species, this behavior could serve as a preadaptive step for a whole series of additional morphological changes aimed at improving or modifying the details of this carriage. The parts most directly involved, the face and the mandibles, should be the areas to undergo the most change. The evolutionary step from simply picking up the female as a courtship manoeuvre to flying with her as a portion of the full epigamic behavior is easily understood when the reproductive advantage of dispersal is considered.

In a recent paper dealing with phoretic copulation in Hymenoptera, Evans (1969) suggested that the dispersal capacity which seemingly has been lost in the groups with wingless females is maintained in some species by the male carrying the female in flight during copulation, by means of their affixed genitalia. He argued that this phoretic behavior should have a high selective advantage, since it would enable the dispersal of the wingless females to new, unexploited populations. He presented examples of such behavior from the Bethyliidae and thynnine and myrmosine Tiphthiidae, and noted that phoretic copulation may also occur in *Timulla*

(Mutillidae). Evans' arguments for the selective advantage of genitalic transport in these wasps should hold equally well for the mandibular carriage discussed in this paper.

The full extent to which the male's mandibles are utilized in the courtship of Mutillidae is unknown. Considering the details of the structure of the head, however, it would seem unlikely that extensive use is made of mandibular carriage in certain groups. For example, in *Dasymutilla occidentalis* (Linnaeus) there are no obvious modifications of either the mandibles or the clypeus which would suggest such usage; indeed, there is a pair of horn-like projections arising from the clypeus in the same area which is concave in species of *Timulla*. These projections would seem to interfere with the male's grasping the female in the manner of *T. dubitata*. At the present time information about the courtship behavior of only a few species of *Smicromyrme*, *Sphacrophthalma*, and *Timulla* is known. In these species we now know that there is a close correlation between certain aspects of their courtship behavior and the structure of the male's mandibles and clypeus. It is likely that a study of the morphology of these structures in species of other genera will predict information about their courtship behavior.

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2.0016 Sexual dimorphism head structure Mutillidae possible behavior explanation.

ABSTRACT.—The presence of a marked sexual dimorphism involving the surface of the clypeus and the mandibular structure occurs in males of certain genera of Mutillidae. These modifications appear to be correlated with a portion of the courtship behavior in which the male grasps the female with his mandibles. In some species the male is known to carry the female in flight while grasping her in his mandibles, thus providing a means of dispersal otherwise unavailable to the wingless females.—J. K. SHELDON

Descriptors: Hymenoptera; Mutillidae; Head; Sexual dimorphism; behavior.